Biological Conservation 206 (2017) 37–46

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/bioc

Review

After the epidemic: Ongoing declines, stabilizations and recoveries in amphibians afflicted by chytridiomycosis

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ARTICLE INFO

Article history:
Received 16 August 2016
Received in revised form 2 December 2016
Accepted 8 December 2016
Available online 23 December 2016

Keywords:
Amphibian
Chytrid fungus
Extinction
Recovery
Wildlife disease

ABSTRACT

The impacts of pathogen emergence in naïve hosts can be catastrophic, and pathogen spread now ranks as a major threat to biodiversity. However, pathogen impacts can persist for decades after epidemics and produce variable host outcomes. Chytridiomycosis in amphibians (caused by the fungal pathogen *Batrachochytrium dendrobatidis*, Bd) is an exemplar, with impacts ranging from rapid population crashes and extinctions, to population declines and subsequent recoveries. Here, we investigate long-term impacts associated with chytridiomycosis in Australia. We conducted a continent-wide assessment of the disease, reviewing data collected since the arrival of Bd in about 1978, to assess and characterize mechanisms driving past, present and future impacts. We found chytridiomycosis to be implicated in the extinction or decline of 43 of Australia's 238 amphibian species. Population trajectories of declined species are highly variable; six species are experiencing ongoing declines, eight species are apparently stable and 11 species are recovering. Our results highlight that while some species are expanding, Bd continues to threaten species long after its emergence. Australian case-studies and synthesis of the global chytridiomycosis literature suggests that amphibian reservoir hosts are associated with continued declines in endemically infected populations, while population stability is promoted by environmental conditions that restrict Bd impact, and maintenance of high recruitment capacity that can offset mortality. Host genetic adaptation or decreased pathogen virulence may facilitate species recovery, but neither has been empirically demonstrated. Understanding processes that influence Bd-host dynamics and population persistence is crucial for assessing species extinction risk and identifying strategies to conserve disease-threatened species.

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http://dx.doi.org/10.1016/j.biocon.2016.12.010

1. Introduction

Wildlife disease is implicated as a key driver of species extinction (e.g. Daszak et al., 2000; Fisher et al., 2012). In the past decade, disease-driven mass declines have been reported across many groups, including amphibians, reptiles, birds, mammals, fishes and corals (Fisher et al., 2012; Lorch et al., 2015; Tompkins et al., 2015). Immediate effects of outbreaks due to pathogen emergence in naïve wildlife populations can be severe and overt (e.g. Blehert et al., 2009). In contrast, long-term disease impacts are more complex, dynamic and much harder to detect and assess. This is especially true when field studies have been initiated decades after the emergence of the pathogen, and pre-arrival records are lacking, such as for avian malaria (*Plasmodium relictum*) in Hawaiian birds (van Riper et al., 1986) and big-horn sheep pneumonia (*Mycoplasma ovipneumoniae*) in the Rocky Mountains (Besser et al., 2013). Host-pathogen coevolution theory postulates that a shift from epidemic to endemic states is generally associated with reduced pathogenicity, underpinned by increased host tolerance, resistance and/or reduced pathogen virulence (de Castro and Bolker, 2005). However, whether such shifts apply to generalist pathogens currently impacting biodiversity is uncertain. Generalist pathogens commonly persist in biotic reservoirs, potentially maintaining high disease impact in a sub-set of highly susceptible host species (de Castro and Bolker, 2005). As recently emerged pathogens become endemic in their new hosts and ranges, understanding the threat associated with ongoing pathogen presence is crucial for assessing impacts and informing conservation actions.

One of the most devastating diseases impacting wildlife over recent decades is amphibian chytridiomycosis, caused by the fungal skin pathogen *Batrachochytrium dendrobatidis* ('Bd') (Berger et al., 1998). Since its discovery, chytridiomycosis has been implicated in the decline of >200 amphibian species, with declines attributed to the pathogen beginning in the 1970s (Skerratt et al., 2007). Bd infection has been reported in >500 amphibian species (Olson et al., 2013) and although the origin of Bd remains unresolved (Rosenblum et al., 2013), it appears to be present in most climatically suitable regions worldwide (Olson et al., 2013).

The introduction of Bd into susceptible, naïve amphibian populations is characterized by a rapid, simultaneous increase in prevalence and infection intensity, followed by mass mortality and population decline (Lips et al., 2006; Vredenburg et al., 2010). If some individuals survive the initial epidemic, Bd may persist as an endemic pathogen in remnant populations or in resistant species that did not decline (Briggs et al., 2010; Murray et al., 2009; Reeder et al., 2012). Host impacts associated with endemic Bd are variable, with some species experiencing substantial ongoing mortality (Murray et al., 2009; Pilliod et al., 2010; Scheele et al., 2016b), which suppresses population abundance, while other species are stabilizing or beginning to recover (Newell et al., 2013; Scheele et al., 2015b). These variable host responses mean that the long-term threat associated with Bd remains uncertain across many parts of the globe.

Here, we investigate long-term host responses to Bd and mechanisms that influence Bd dynamics in declined species. First, using a continental-scale assessment of Australian amphibians, we review the impacts of chytridiomycosis 37 years post-Bd emergence. We categorize impacted species based on severity of decline, ongoing disease impact and whether population recovery has been observed. Chytridiomycosis was first reported in 1998 in Australia (Berger et al., 1998) and has subsequently been extensively studied across a large number of host species and environmental and climatic conditions (Berger et al., 2016). Recent reviews have focused on identifying actions, research and resources needed to prevent extinctions in threatened Australian frogs (Skerratt et al., 2016) and overviewed the taxonomy, phylogeny, distribution and ecology of Bd (Berger et al., 2016). However, a comprehensive assessment of Bd impacts and long-term population trajectories has not been undertaken, for Australia or other countries. We also review mechanisms and processes that influence endemic Bd dynamics across the globe to better understand factors underlying initial and ongoing disease impacts, incorporating case-studies of Australian species. Our focus on long-term host responses provides new insights into Bd impacts several decades post-emergence, and identifies the processes underlying variable host responses.

2. Chytridiomycosis in Australia: past and present

Some of the earliest reports of enigmatic amphibian declines globally were from eastern Australia, with disappearances of rainforest species first documented in 1979 (Skerratt et al., 2007). Over the following decades dramatic declines were reported in other tropical and temperate species in eastern Australia (Laurance et al., 1996; Osborne, 1989). The unprecedented decline of multiple species across geographic regions and an initial lack of a causal mechanism resulted in considerable debate on the extent and cause(s) of declines (Campbell, 1999). In 1993, frog mortalities were observed in the Australian wet tropics, both in the wild and following an experimental translocation of the sharp-snouted day frog (*Taudactylus acutirostris*) (Dennis and Mahony, 1994; Mahony et al., 1999; Speare, 1995). Due to concern about the potential extinction of *T. acutirostris*, the establishment of a captive insurance colony was attempted in 1993; however, most individuals died soon after being brought into captivity (Banks and McCracken, 2002). Deaths of wild and captive frogs were associated with a skin infection that was later identified as the novel disease, chytridiomycosis (Banks and McCracken, 2002; Berger et al., 1998). The disease hypothesis remained controversial, even after experimental transmission and the description of outbreaks causing mass mortalities of wild frogs in Australia and Central America in 1998 (Berger et al., 1998). Disease spread was not widely supported as the cause of declines until multiple lines of evidence (epidemiological, pathological, theoretical and experimental) were collated and repeated field and laboratory studies were conducted, both in Australia and globally (Berger et al., 2016; Skerratt et al., 2007; Wake and Vredenburg, 2008).

The absence of Bd in amphibians collected prior to the commencement of population declines strongly indicates that Bd is an introduced pathogen to Australia (Australian Government, 2006; Gillespie et al., 2015; Hunter et al., 2010; Skerratt et al., 2007). Furthermore, unlike in